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A method for estimating the significance of surface dispersal for population fluctuations of Collembola in arable land

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Summary. Recent studies have shown marked differences between Collembola communities in a field and a nearby fallow which had both been managed in a similar manner before management conversion. To investigate the extent to which these differences could be attributed to surface dispersal, small pitfall traps, provided with fences, were used to determine directions of dispersal.
The dominant Collembola trapped in pitfalls were *Isotomurus palustris*, *Lepidocyrtus cyaneus* and Sminthuridae. *Isotoma viridis* and the Genus *Folsomia* were subdominant or seldom caught in pitfall traps. The number of Collembola trapped in pitfalls decreased from field to fallow, suggesting a lower activity under more favourable conditions in the fallow. The dispersal direction of Collembola depended on barrier position (field, borderline, or fallow). The most striking differences between the soil communities, within the Genus *Folsomia*, could not be assigned to surface dispersal, whereas the higher or increasing proportions of *Isotomurus palustris* and Sminthuridae in the fallow compared to the wheat field could partly be explained by migration.

Key words: Collembola, dispersal, pitfall traps, agro-ecosystems, methods

Introduction

Many studies have dealt with distribution and dispersal of Collembola. Directed migration has been shown to be triggered mainly by temperature, humidity, food availability, competition, and pheromones (Christiansen 1970; Joosse & Verhoef 1974; Kaczmarek 1978; Fábián & Petersen 1994; Bengtsson et al. 1994b). Investigations of horizontal and vertical patterns of soil-inhabiting Collembola (e.g. Usher 1985; Bauer & Christian 1993; Faber & Joosse 1993) indicate that edaphic forms cover only small distances, e.g. less than 10 cm per day. Petersen (1978) found that two populations, within a distance of 14 m, were separated clearly genetically. Therefore it is unlikely that migration within the soil has an effect on population fluctuations at more distant sampling sites. They may, however, be influenced by surface dispersal.

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Since most studies on Collembola dispersal were carried out under laboratory conditions, "we clearly need (...) some basic knowledge of their dispersal ecology" (Bengtsson et al. 1994a). Very little is known about the dispersal of epigeic species. Surface active species can either be passively distributed by wind or runoff water (Usher 1985; Dunger & Engelmann 1978; Christiansen 1964), or they migrate actively. Besides observations on mass migrations (Christiansen 1964, and references therein) data on directed migration are sparse. Hågvar (1995) observed directional movements, of over 200–300 m per day, of *Hypogastrura socialis* on snow. Direct observation is the only technique which allows investigation of active migration, since even mark-recapture methods cannot distinguish between active and passive dispersal. However, direct observation is extremely time-consuming, and therefore indirect methods – e.g. pitfall traps – must be used in order to estimate collembolan dispersal.

The horizontal distribution of hemiedaphic Collembola can be influenced by surface dispersal. Filser (1991, 1995) showed that the abundances of *Isotomurus palustris*, in the soil were lower in plant rows than in interrows, whereas the numbers caught in pitfall traps were always higher in the rows. This was probably due to increased activity as an effect of searching for a more favourable microhabitat. However, these investigations were carried out with large pitfall traps (diameter: 16 cm), so that wind dispersal may have had a major influence on the numbers caught (Dunger & Engelmann 1978). Biases, caused by wind dispersal, can be reduced by minimising the trap size (Kampichler, pers. comm.). Small pitfall traps have been shown to be a reliable and practical method of sampling Collembola but "underscore the need of further basic research on pitfall trapping of Collembola" (Berbiers et al. 1989).

Several studies have reported shifts in the dominance structure of Collembola after management conversion (e.g. Brussaard et al. 1988; Filser et al. 1996a). Possible reasons for such structural changes are microclimatic conditions, food availability and quality, predation, competition, passive dispersal and migration. The purpose of this study was to elucidate to what extent surface dispersal might contribute to population fluctuations of Collembola in arable land. As an example, the dispersal of epigeic Collembola between an arable field and a nearby fallow that recently had been set aside was investigated. Small pitfall traps provided with fences were used. These were positioned in a special arrangement in order to determine the dispersal direction of the Collembola.

Materials and Methods

The studies were carried out at the experimental farm of the FAM (Forschungsverbund Agrarökosysteme München) research network on agroecosystems 40 km North of Munich. Mean annual precipitation is 833 mm; mean annual temperature 7.5 °C. The field (dystric eutrochept) and the fallow (typic udifluvent) are both fine-loamy, mixed, mesic soils with nearly identical properties in the (former) plough layer. Before management conversion, in September 1992, both plots had been cropped with winter wheat (1991) and spring barley (1992). The field was cropped with wheat (1993), corn (1994), and winter wheat (1995). In winter it was under catch crops (mustard). Except for seed drilling, no tillage took place. The vegetation of the fallow has been left to natural succession since autumn 1992.

The soil Collembola were sampled between May 1994 and May 1996 with a corer (6.8 cm diameter) and five replicates per site. The cores were divided into subsamples (0–5, 5–10, 10–15, 15–20 cm depth) and extracted within seven days using a modified Macfadyen extractor (Filser 1992). Ethylene glycol served as collection fluid.

In order to investigate the direction of dispersal of epigeic Collembola transparent polyethylene barriers connected by black adhesive tape were used with the traps (Fig. 1). Where necessary, the vegetation under the barriers was cut to 10 cm. A transect of three parallel barriers was installed, one in the wheat field, one in the fallow, and one at the borderline between both habitats. The distance between two barriers was 7 m. They were equipped with five small pitfall traps (2 ml reaction vessels, Fa. Eppendorf, Hamburg) at each side to allow discriminating between the directions of movement. Each of these was filled with 750 µl ethylene glycol with an admixture (0.3 %) of Deconex (Fa. Borer Chemie, CH-4528 Zuchwil), an odourless detergent.

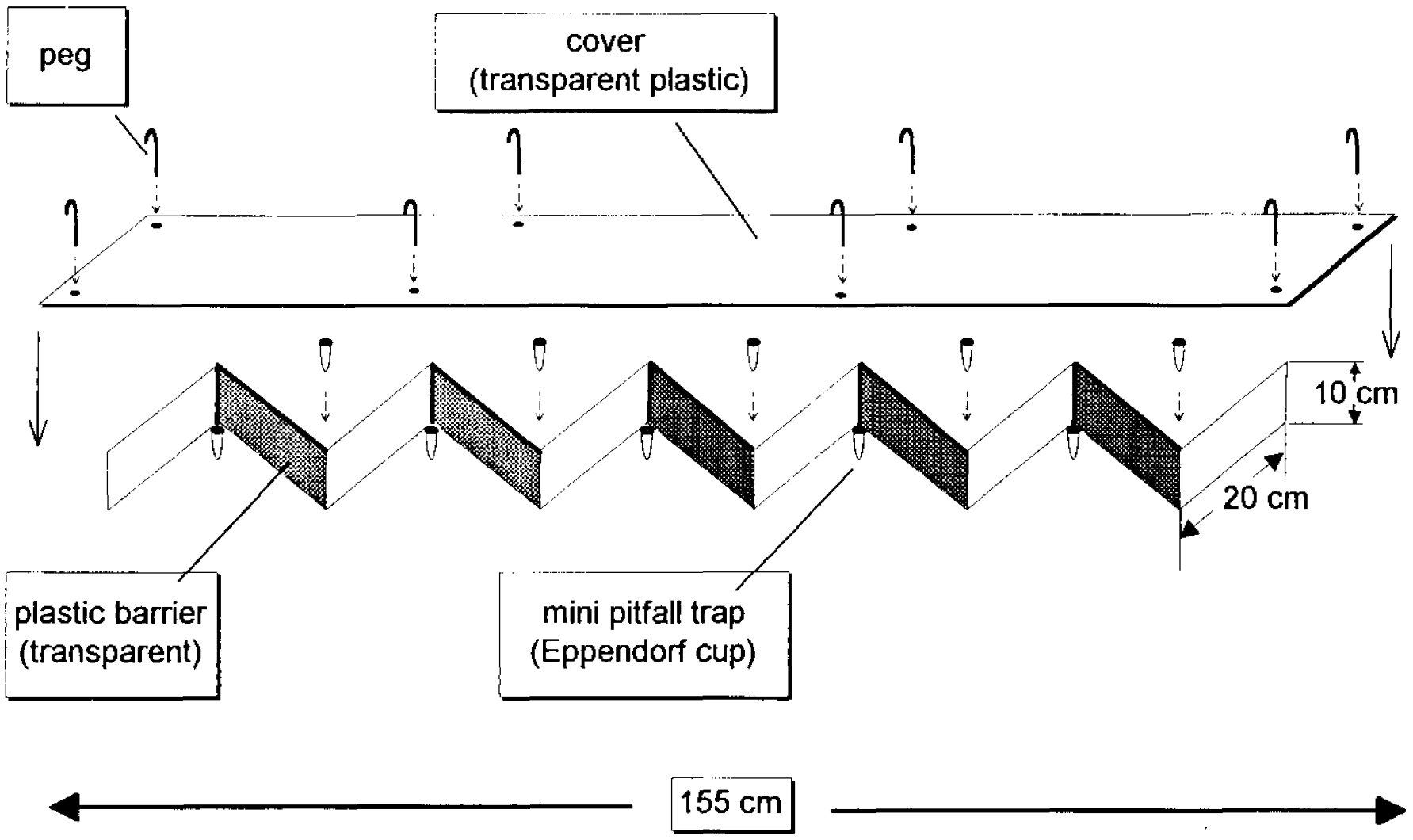

Fig. 1. Experimental design of small pitfall traps for estimating the dispersal of Collembola

At the beginning of each pitfall sampling interval in early spring (27 March–4 April 1995), late spring (11 May–18 May 1995) and summer (22 June–1 July 1995), soil samples were taken and analysed for edaphic Collembola. All of them were mounted on slides using Hoyer's mixture (Dunger & Fiedler 1989), and identified to species according to Gisin (1960), Palissa (1964), Fjellberg (1980), Dunger & Zivadinovic (1989), and Zimdars & Dunger (1994).

Results

The soil inhabiting populations of *Folsomia manolachei* Bagnall 1931 (sensu Deharveng 1982), *Isotomurus palustris* (Müller 1776), *Lepidocyrtus cyaneus* Tullberg 1871 and Sminthuridae were larger in the fallow (Table 1). *Folsomia quadrioculata* (Tullberg 1871) was more abundant in the field.

Table 1. Significant differences (Mann-Whitney U Test) between abundances of selected Collembola in field and fallow soil in 0–20 cm depth

	Folsomia quadrioculata	*Folsomia manolachei*	*Isotomurus palustris*	*Lepidocyrtus cyaneus*	Sminthuridae
May 1994	##		*		
Jul 1994	##	**	**	*	
Aug 1994	##	*	*		
Oct 1994	#	**	**	*	
Nov 1994	##	**	**		
Feb 1995		**	*	**	**
Mar 1995		**		**	
May 1995		**			*
Jun 1995		**		**	*
Aug 1995				**	
field, average abundance/m²	3,943	33	942	783	569
fallow, average abundance/m²	655	2,555	5,056	1,950	1,702

Crosses indicate higher abundances in the field: # $p<0.05$; ## $p<0.01$. Asterisks indicate higher abundances in the fallow: * $p<0.05$; ** $p<0.01$

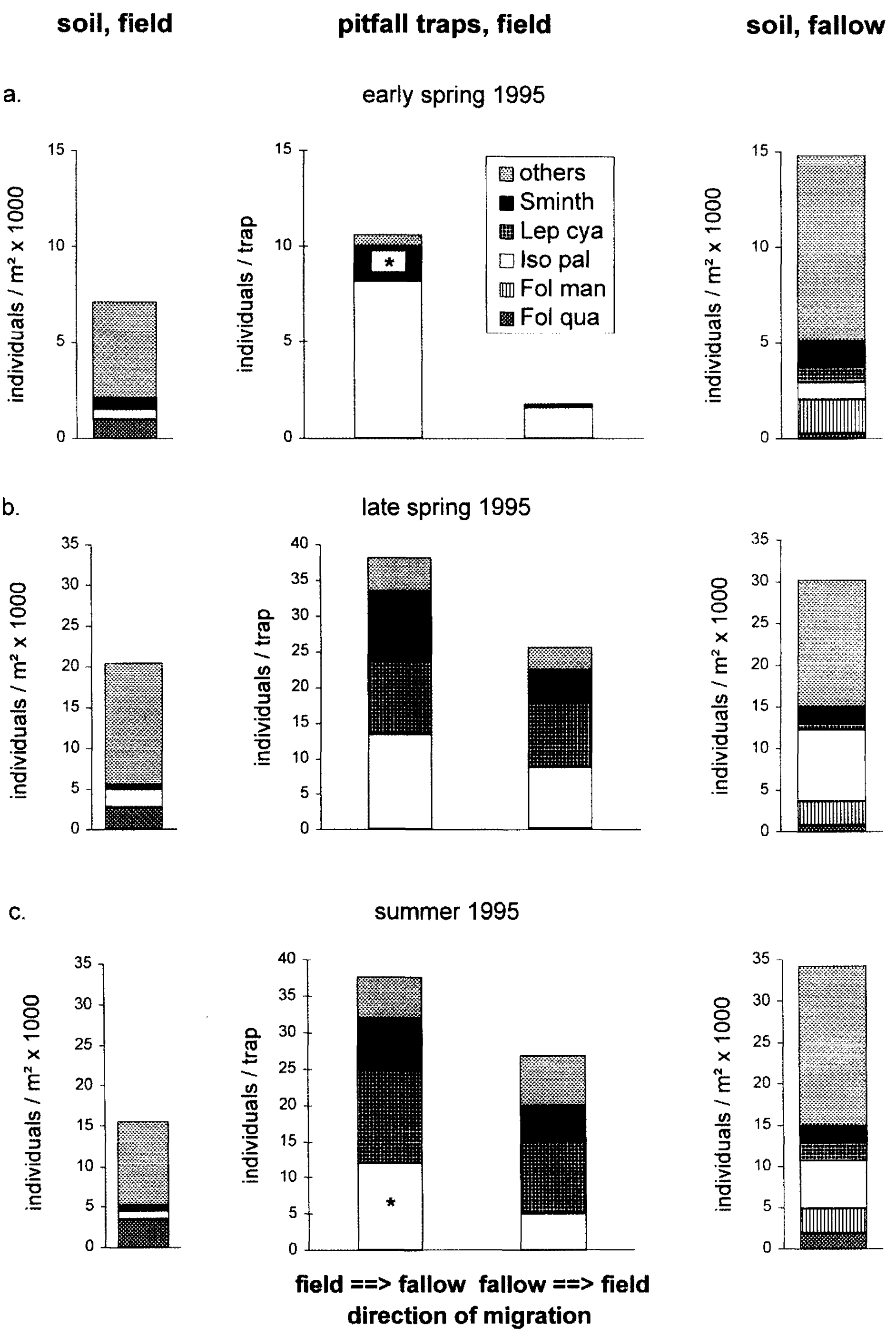

Fig. 2. Mean abundances (n = 5) of Collembola in field and fallow soil (0–20 cm depth) and in pitfall traps at different sampling times at the field barrier (note different scales). Significant differences in soil see Table 1, significant differences in pitfall traps (Mann-Whitney U test). * $p < 0.05$. Fol qua = *Folsomia quadrioculata*, Fol man = *Folsomia manolachei*, Fol juv = juvenile *Folsomia*, Iso pal = *Isotomurus palustris*, Lep cya = *Lepidocyrtus cyaneus*, Sminth = Sminthuridae

The overall abundances of Collembola increased from early to late spring (Fig. 2). At the barrier in the field more animals were found in the direction of dispersal from field to fallow on all sampling intervals. This was true for *I. palustris* and the Sminthuridae. Only one individual of the genus *Folsomia* was captured.
In spring, the total number of Collembola trapped in both directions of dispersal decreased from field to fallow, but there was no consistent general migration pattern (Fig. 2, 3). In contrast to the field barrier, at the borderline and fallow barrier more individuals of *I. palustris* dispersed from fallow to field than in the other direction.

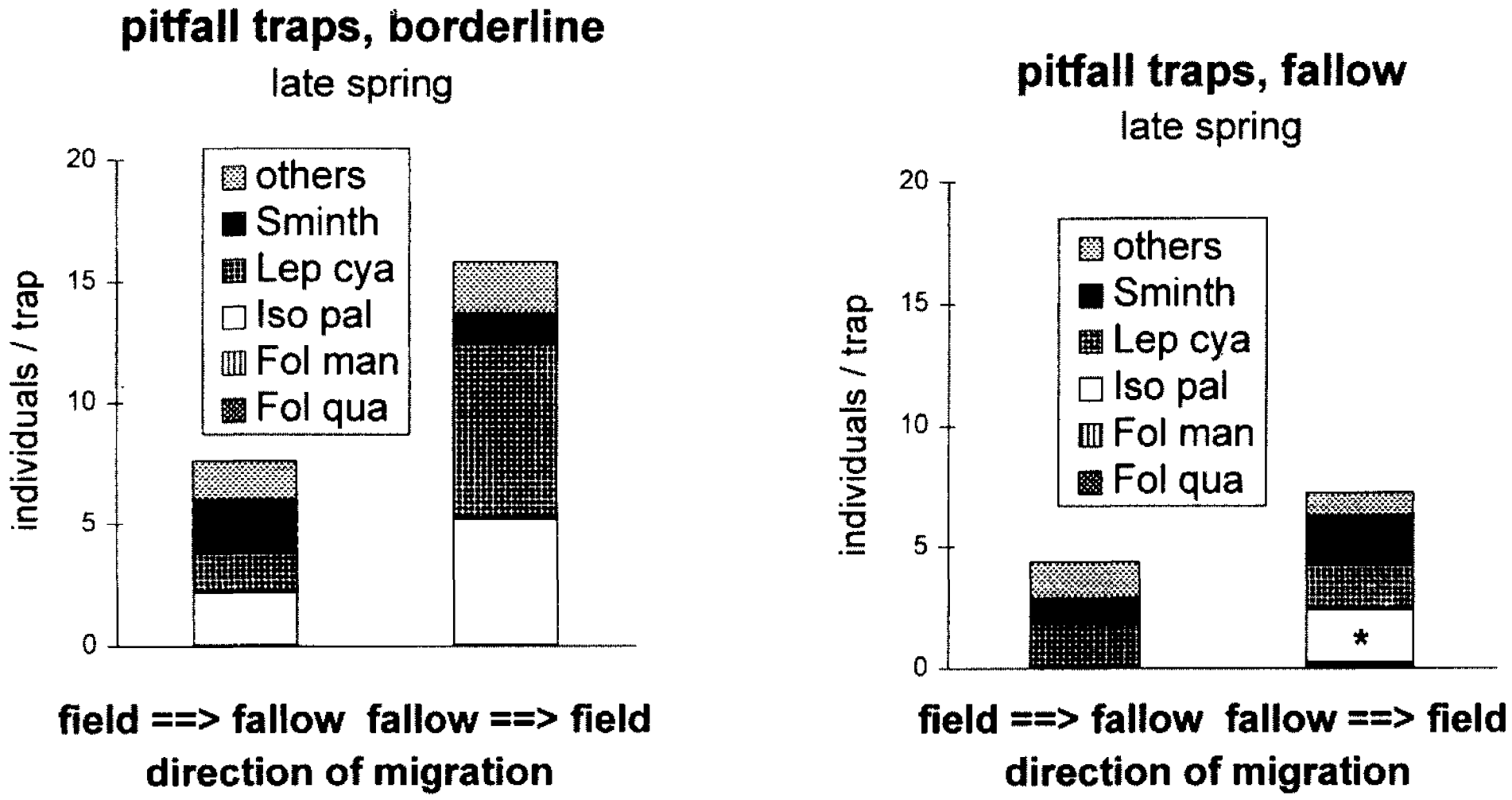

Fig. 3. Mean abundances (n = 5) of Collembola in pitfall traps (late spring) at the borderline and fallow barriers. Further explanations see Fig. 2. For abbreviations see Fig. 2

Discussion

Method

The small trap size, the roofs covering them, and the dense vegetation in the habitats examined should have restricted the trapping of animals dispersed by wind to a minimum (Dunger & Engelmann 1978; Berbiers et al. 1989). Dispersal by runoff water could also be dismissed, because the small pitfall traps would have overflowed and the contents discarded. In addition, one can assume that passive dispersal should be similar for species with comparable habitat, size and morphology such as *I. palustris* and *I. viridis*. However, *I. palustris* (Fig. 2) dispersed from field to fallow but *I. viridis* showed no significant differences in dispersal directions. Therefore we postulate that our sampling design is appropriate to estimate migration rather than passive dispersal.

Surface activity

L. cyaneus, *I. palustris* and the Sminthuridae were the dominant taxa in the pitfall traps and together accounted for between 74 and 92 % of the Collembola caught in pitfall traps. Both *Folsomia* species were found almost exclusively in the soil. Despite its high surface activity,

no significant differences were found between the directions of dispersal of *L. cyaneus* at any locations or sampling dates. This implies that the higher abundances of this species in the fallow soil must be attributed to higher reproduction or lower mortality rather than to migration as if it had been caused by passive dispersal the same phenomenon should have been found for other hemiedaphic species. In fact, predator numbers were higher in the field (Filser et al. 1996b), whereas the most important food source of *L. cyaneus*, soil fungi, had a higher biomass in the fallow (Filser et al. 1996a). The greater abundance of *F. manolachei* in the fallow could not be attributed to active or passive dispersal, because this species showed no surface activity in the experimental plots and the differences may be accounted for by factors similar to those indicated for *L. cyaneus*. *F. quadrioculata* was the only species that occurred more frequently in the field. It is remarkable that this species showed no surface activity on any of the three sampling dates, since under comparable microclimatic conditions it "was often seen crawling about on the vegetation of the Level Pasture in astonishing numbers" (Haarlov 1960). Due to the lack of evidence for migration between the habitats, *F. quadrioculata* may have profited from reduced competition due to lower abundances of other Collembola (Bengtsson 1994a). This hypothesis is also supported by the fact that it was practically absent in the fallow even though it had been found in this site before it had been set aside in 1992 (Filser et al. 1996b).

Migration

The patterns obtained for *I. palustris* and Sminthuridae were similar: In the field they preferentially migrated towards the fallow, whereas in the fallow the other direction was preferred. The preference of *I. palustris* for moist habitats is the most probable explanation for its increased abundance in the fallow whereas many Sminthuridae are pollen feeders (Gisin 1960; Fjellberg 1980) and food availability was higher in the fallow than in the arable field, which was kept free of flourishing vegetation other than the crop. The lower vegetation density in the field probably also promoted the much higher overall activity than in the fallow. Thus, more Collembola must have moved towards the fallow than to the other direction. Therefore, the higher numbers of Sminthuridae and *I. palustris* in the fallow soil (cf. Fig. 2) can partly be attributed to migration.

Placement effects

The most obvious placement effect of our pitfall barriers was the generally decreasing Collembola numbers from the field to the fallow. Together with the fact that the Collembola abundances in soil, except for *F. quadrioculata*, were generally lower in the field we may conclude that the high surface activity in the field was an effect of unfavourable conditions. This may have been true in the field compared to the fallow for several reasons. The most important ones are drought (Joosse & Verhoef 1974; Bauer & Christian 1993), habitat patchiness (Bengtsson et al. 1994a), food shortage (Verhoef & Nagelkerke 1977; Bengtsson et al. 1994a), agrochemicals (Fábián & Petersen 1994), or predators (Christiansen 1964). At the fallow barrier, the Collembola often tended to migrate back towards the field. This may be explained by competition (Bengtsson et al. 1994a, b) as an effect of the higher overall abundances compared to the field.

Conclusions

We conclude that our sampling design is appropriate for testing the migration of Collembola in habitats with comparable surface structure. In environments with less vegetation cover wind dispersal may have a larger influence on the numbers caught by the traps (Dunger & Engelmann 1978). In contrast to other studies, no surface activity of *F. quadrio-*

culata was observed. Despite high surface activity, *L. cyaneus* did not show directed dispersal. For Sminthuridae and *I. palustris* migration to more favourable habitats could be assumed.

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